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Climatic effects on timing of spring migration and breeding in a long-distance migrant, the pied flycatcher *Ficedula hypoleuca*

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Both, C., Bijlsma, R. G. and Visser, M. E. 2005. Climatic effects on spring migration and breeding in a long-distance migrant, the pied flycatcher *Ficedula hypoleuca*. – J. Avian. Biol. 36: 368–373.

Climate change has advanced the breeding dates of many bird species, but for few species we know whether this advancement is sufficient to track the advancement of the underlying levels of the food chain. For the long-distance migratory pied flycatcher *Ficedula hypoleuca* the advancement in breeding time has been insufficient to maintain the synchrony with their main food sources. The timing of arrival in the breeding areas from their African wintering grounds is likely to constrain the advancement of breeding date. We hypothesise that this is because in Africa they cannot predict the advancement of spring in their breeding habitat. However, long-distance migrants may advance their arrival time by migrating faster when circumstances en route are favourable. In this study we show that both arrival and breeding date depend on temperatures at their main North African staging grounds, as well as on temperature at the breeding grounds. Male arrival and average laying date were not correlated, but the positive effect of temperature in North Africa on breeding dates suggests that breeding date is indeed constrained by arrival of females. Long-distance migrants thus are able to adjust arrival and hence breeding by faster spring migration, but the degree of adjustment is probably limited as timing schedules in spring are tight. Furthermore, as climate change is affecting temperatures differently along the migratory flyway and the breeding areas, it is unlikely that arrival dates are advanced at the same rate as the timing of breeding should advance, given the advancement of the underlying levels of the food chain.

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Many organisms have advanced their phenology during the last decades (Crick et al. 1997, Winkel and Hudde 1997, Parmesan and Yohe 2003), but we have only a limited notion of the mechanisms behind these changes, and what the consequences are of the observed changes (Visser et al. 1998, Both and Visser 2001). The ultimate reason for the advancement of laying date in birds probably lies in the advancement

of other parts of the food chain. Long-distance migrants may have difficulties to adjust their breeding cycle to changes in their main food sources because they rely on a sequence of areas during migration that may change at different rates (Drent et al. 2003), and which may not provide information on the phenological state of their breeding areas (Coppack and Both 2002).

In a previous paper we showed that the long-distance migratory pied flycatcher *Ficedula hypoleuca* has advanced its breeding date, but not sufficiently to track the advancement of their main food sources (Both and Visser 2001). We argued that at their African wintering grounds these birds cannot predict when spring starts on their breeding grounds, and that as a consequence spring arrival had not changed over the years. This is at variance with other studies on long-distance migrants that reported advancements in arrival date (Bradley et al. 1999), including pied flycatchers migrating to Scandinavia (Hüppop and Hüppop 2003). Recent data showed that arrival dates in some species of sub-Saharan migrants correlate with circumstances at the wintering grounds (Cotton 2003, Sokolov and Kosarev 2003) and en route (Huin and Sparks 1998, 2000, Forchhammer et al. 2002, Saino et al. 2004), which opens the possibility that climate change, via improved conditions en route, can advance spring arrival. Hence, timing of migration may not constrain adaptation to climate change as much as we suggested in our earlier work (Both and Visser 2001).

In this paper we estimate to what extent arrival and breeding dates are correlated with the temperatures en route and in the breeding area. If there are such correlations, arrival dates may advance with a further increase in spring temperatures.

Methods

Ring recovery data

We used all data of pied flycatchers, recorded at the Dutch Bird Ringing Centre that were ringed as nestling or breeding adult in The Netherlands, and that were recovered dead between February 1 and June 30. We included only birds that were recovered at least 100 kilometres from the ringing site and that were not recovered while breeding. The records used were thus Dutch breeding birds on their spring migration to The Netherlands. No records south of the Sahara were available from the winter period.

Arrival dates

One of us (RB) recorded during each year the arrival date of the first arriving five (1969–1971) or ten (since 1972) male pied flycatchers. The data come from two different areas: from 1969 to 1990 on the southern Veluwe area (Central Netherlands, 5°45'E, 52°02'N), and from 1991 to 2003 in Drenthe (North Netherlands, 6°17'E, 52°52'N). Both areas were visited on an almost daily basis throughout the year and especially frequently during spring and summer (from late February and onwards). The study areas on Veluwe and Drenthe are

forested with (partly non-native) conifers and interspersed with smaller pockets of deciduous woodland. Arrival dates of males, here expressed by singing birds, in both areas are probably accurate, given the intensity of the observer's presence. For instance, when birds were seen before any song was heard, singing was always recorded later the same day.

The distance between both areas is approximately 100 km. Because we have the longest dataset for the first five males and the average date for the first five and first ten males was strongly correlated ($r=0.98$, $n=32$ (1972–2003), $P<0.0001$), we used only the data for the first five males in each year. We corrected statistically for the change in study area by always including an area effect in the analysis. Additionally, we have accurate arrival dates of the first male at our nest box study area, the Hoge Veluwe, for nine years between 1992–2003, and in this small sample arrival dates in both areas tended to be positively correlated ($r=0.62$, $n=9$, $P=0.07$), which strengthens our view that we can combine both datasets.

Laying dates

Laying dates were collected since 1960 on the Hoge Veluwe area (5°51'E, 52°02'N), which is approximately 5 km east of the area where the arrival dates were collected. About 400 nest boxes were present, which were checked weekly. Laying dates were estimated on the assumption that one egg was laid every day. In the analyses we included only first broods, excluding all broods of females known to have laid earlier during the same year and broods started more than 30 days after the first egg in that year. For 1994–2003 laying dates were also collected for about five pairs in nest boxes in the Drenthe area, where arrival dates were collected in 1991–2003.

Temperature data

Mean monthly temperatures were obtained from the website <http://iridl.ldeo.columbia.edu/SOURCES/NOAA/NCDC/GHCN/v2/>. We used data from Gibraltar (5°35'W, 6°15'N) and Casablanca, Morocco (7°67'W, 33°57'N), because most recoveries were in the area in between these two stations, with few recoveries more to the east (Fig. 1). We averaged data for these two stations to get a more regional temperature. In the analysis of arrival of the first males we used the mean monthly temperatures for March, because the first birds were recovered in March in North Africa. In the analysis of annual breeding date we used the average temperature for March and April, because this covers most of the period the birds were recovered in North Africa.



Fig. 1. Recovery sites of pied flycatchers ringed as nestlings or breeding in The Netherlands during spring migration. The size of the dots shows the number of recoveries: 1, 2, 3 and 19 recoveries per 1-degree block.

For The Netherlands we used data collected by the Royal Dutch Meteorological Office in De Bilt, about 50 kilometres west of our study area. The mean daily temperature in the period March 16–April 15 (NL1) was used as local temperature that may affect arrival. For laying date we used the mean daily temperatures in the period April 16–May 15 (NL2) (Both et al. 2004). Correlations between Dutch and African temperatures were: NL1–NL2: $r = -0.009$, $n = 35$, $P = 0.96$; NL1–North Africa March: $r = 0.28$, $n = 34$, $P = 0.11$; NL2–North Africa March: $r = 0.41$, $n = 34$, $P = 0.015$; NL1–North Africa March–April: $r = 0.17$, $n = 32$, $P = 0.36$; NL2–North Africa March–April: $r = 0.33$, $n = 32$, $P = 0.069$.

Analyses

The effects of temperatures on arrival and breeding dates were analysed with multiple regression including both temperatures from the breeding area and from the two weather stations in North Africa, as well as a factor to account for the change in study area for arrival dates. Only main effects were fitted in the model, and a backwards procedure was performed. Degrees of freedom do not always add up, because of some missing data for temperatures of some weather stations.

Results

Ring recoveries

In spring, Dutch pied flycatchers were recovered from North Africa (mainly Morocco) from March 2 until June 27 (median April 19, $n = 60$). In this area (27° – $36^{\circ}5'N$),

first-year birds were recovered significantly later than older birds (median first-year: April 22, $U = 567.5$, $n = 31$; median older birds: April 14, $U = 238.5$, $n = 26$, $P = 0.0086$ (contrary to Lundberg and Alatalo 1992)).

Arrival and breeding dates

In most years the arrival of the first five males on the Southern Veluwe and Drenthe was highly synchronous (median interval between first and fifth male was 3 days, range 1–15 days). Mean arrival of the first five males varied between years from April 2 to April 26 (median April 18). Interestingly the median arrival date over all years is one day ahead of the median passage date through North Africa.

Breeding dates on the Southern Veluwe varied between May 3 and May 19 (median May 11). It took on average 21 days from the median recovery date in North Africa to the annual mean breeding date. The mean breeding dates of the small sample from Drenthe tended to be positively correlated with the Veluwe breeding dates ($r = 0.56$, $n = 10$, $P = 0.10$), confirming other data that laying dates covary over larger spatial scales (Both et al. 2004).

Breeding dates and male arrival dates were not correlated (whole material: $r = 0.006$, $n = 35$, $P = 0.97$, Veluwe area only: $r = 0.066$, $n = 22$, $P = 0.77$, Drenthe data only: $r = -0.19$, $n = 10$, $P = 0.59$). If we restrict our analysis for the mean laying date of the first five nests in each year, which may make a better comparison between the first arriving males and the first arriving females, there was still no correlation between male arrival and breeding date (whole material: $r = 0.054$, $n = 35$, $P = 0.76$).

Environmental effects on arrival

Males arrived earlier in years with higher temperatures in both the breeding area and at their stop-over site in North Africa (Fig. 2). March temperatures in North Africa did increase over the years ($r = 0.70$, $n = 34$, $P < 0.001$), as did the Dutch temperature between March 16 and April 15 ($r = 0.38$, $n = 35$, $P = 0.025$), suggesting that circumstances en route and during arrival at the breeding grounds have improved over the years. This is reflected in a tendency of advanced arrival of the first five males over the years ($F_{1,33} = 3.61$, $P = 0.066$).

Environmental effects on breeding

The average breeding dates are strongly correlated with temperatures on the breeding grounds and additionally

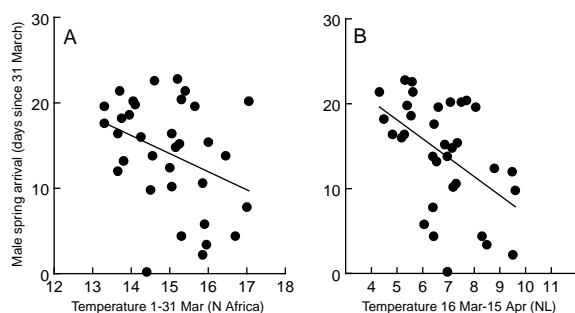


Fig. 2. The effect of temperature en route in North Africa (A) and during arrival in The Netherlands (B) on the average arrival date of the first five pied flycatcher males. ANCOVA: Area $F_{1,30} = 2.04$, $P = 0.26$, Temperature Netherlands (16 March–15 April) $F_{1,30} = 9.32$, $P = 0.005$, Temperature North Africa (1–31 March): $F_{1,30} = 4.18$, $P = 0.049$, R^2 full model: 0.34.

with temperatures during migration in North Africa (Fig. 3). March – April temperatures in North Africa did increase over the years ($r = 0.72$, $n = 32$, $P < 0.001$), as did the Dutch temperature between April 16 and May 15 ($r = 0.48$, $n = 35$, $P = 0.004$), again suggesting that circumstances en route and during the start of breeding have improved over the years, which is reflected in an advance of the annual mean laying date over the years ($r = -0.59$, $n = 35$, $P < 0.001$).

Discussion

Pied flycatchers have a tight time schedule during spring, with their mean passage date in North Africa being at about the same time as the first males arrive in the Netherlands, and just about two to four weeks before the average laying date in The Netherlands. We showed that environmental circumstances en route have an effect on the timing of events: males arrived earlier in The Netherlands when temperatures encountered during

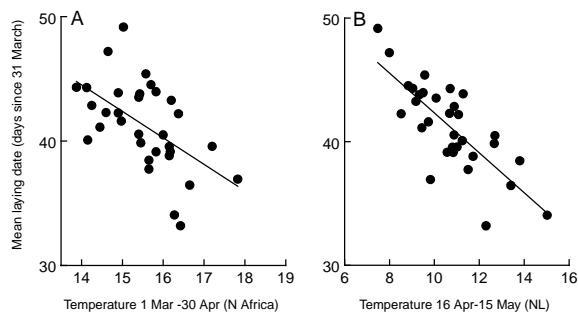


Fig. 3. The effect of temperature en route in North Africa (A) and during the period of egg laying in The Netherlands (B) on the average laying date of pied flycatchers on the Hoge Veluwe. Linear regression: Temperature Netherlands (16 April–15 May): $F_{1,30} = 37.66$, $P < 0.001$, Temperature North Africa (1 March–30 April): $F_{1,30} = 9.87$, $P = 0.004$, R^2 full model: 0.69.

spring migration in North Africa were higher and annual breeding dates were correlated with temperatures in the staging area and the breeding area. Breeding and male arrival dates were not correlated, questioning the mere biological relevance of studies showing earlier arrival in males only (Bradley et al. 1999, Cotton 2003, Sokolov and Kosarev 2003).

Dutch pied flycatchers did not fully adjust to increased spring temperatures and the advance of their food supply, and selection on early breeding increased because spring arrival had not changed (Both and Visser 2001, Coppack and Both 2002). One constraint in advancing spring arrival may be the lack of genetic variation in the birds' spring arrival date, which depends mainly on photoperiodic cues at the wintering grounds (Gwinner 1996, Gwinner and Helm 2003). Although in other species, genetic variation for the timing of migration is present (Pulido et al. 2001, Møller 2001, Pulido and Berthold 2003), spring arrival of pied flycatcher males was neither repeatable nor heritable (Potti 1998). The constrained adjustment to climate change could thus be due to lack of genetic variation.

Favourable circumstances en route and at the breeding site advanced male arrival and breeding date, showing that spring arrival can be advanced as a result of climate change. This may come as a surprise, because on the wintering grounds and en route birds must have difficulty in predicting weather conditions for the breeding site thousands of kilometres away. However, birds may migrate at higher speeds during spells of warm weather (Richardson 1990, Schaub and Jenni 2001, Jenni and Schaub 2003), and the closer birds approach the breeding grounds the more circumstances en route will be correlated with conditions at the breeding grounds. Pied flycatchers have indeed been shown before to arrive later when temperatures en route are low (Curio 1959, Ahola et al. 2004) and even reverse their migration direction from north-east to south-west in spring when temperatures encountered in central Europe are low (Walther and Bingman 1984). Moreover, both in North Africa as in The Netherlands the temperatures have increased in the course of the years to about the same extent (0.052 – $0.075^\circ\text{C}/\text{year}$), as well as in the area in between at the time most flycatchers pass by (mean April temperatures: Tortosa (E): $0.047^\circ\text{C}/\text{year}$, Lyon (F): $0.060^\circ\text{C}/\text{year}$, Klein Tank et al. 2002). Since high temperatures at the breeding grounds are often associated with southerly winds, birds also profit from tail winds, which may increase their flight speed as well (Liechti 1995). Birds thus experience improved (climatic) circumstances during their whole migration route from North Africa to The Netherlands, which may stimulate birds to migrate at a higher speed and consequently arrive earlier at the breeding grounds when temperatures are higher.

The effect of climatic variation in North Africa on breeding dates in The Netherlands suggests that arrival

of females may not be constraining breeding dates as much as we suggested earlier (Both and Visser 2001). However, if the observed correlation with North African temperatures is caused by more rapid migration (as argued above), then this suggests that arrival indeed is a constraint, although not a fixed one, because flycatchers breed earlier when they arrive earlier. The earlier breeding with high North African temperatures may be caused by females either migrating faster and arriving earlier at the breeding grounds, or they arrive at the same time but in better condition and therefore can reduce the interval between arrival and breeding (Marra et al. 1998). In general, pied flycatchers arrive with low body reserves (Silverin 1980, but see Sandberg 1996 for northern breeders) suggesting that high body reserves at arrival do not allow these birds to shorten the time interval between arrival and breeding (Potti 1999), and that the main cause of earlier breeding is faster migration and earlier arrival.

Recently, correlations were found between spring arrival and conditions at the wintering grounds in other sub-Saharan migrants (Cotton 2003, Saino et al. 2004), suggesting that they not only rely on photoperiodic cues (Gwinner 1996, Gwinner and Helm 2003), but also on local environmental circumstances to start their spring migration. These studies, however, did not consider the alternative effects of circumstances en route on arrival date (but see Forchhammer et al. 2002, Hüppop and Hüppop 2003, Sokolov and Kosarev 2003), and direct evidence for environmental determinants of departure from the wintering grounds in trans-Saharan migrants is lacking (Gwinner and Helm 2003).

We show that the improved circumstances en route can speed up long-distance migrants on migration, and advance their arrival and breeding, but this advancement must be constrained by their maximal migration speed and the start of migration from their sub-Saharan wintering grounds. The observation of higher migration speeds, and hence earlier arrival and breeding, must be a temporal solution to ongoing climate change, and further warming forces these long-distance migrants to adapt other parts of their migration behaviour as well (Coppack and Both 2002, Coppack et al. 2003).

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